

THE INHERITANCE OF PHOTOPERIODIC RESPONSE AND TILLERING IN MAIZE-TEOSINTE HYBRIDS¹

JOHN S. ROGERS

Texas Agricultural Experiment Station, College Station, Texas

Received February 1, 1950

THE importance of day length as a determining factor in the time of floral initiation in plants was first reported by GARNER and ALLARD (1920). Since then numerous investigations have been conducted on this phenomenon, and many plants have been classified into short-day, long-day and day-neutral types on the basis of their response to photoperiod. All known varieties of teosinte belong to the short-day group of plants, while North American maize varieties are little influenced by photoperiod, and may be classified as day-neutral types. The fact that fertile hybrids may be readily produced between maize and teosinte affords an excellent opportunity for a study of the inheritance of this short-day character in hybrids between the two species.

PHOTOPERIODISM

The exact physiological processes necessary to bring about the change from a vegetative to a flowering state are still unknown, despite the considerable information on this subject which has now been collected. Although several factors may influence the formation of flower primordia, it is generally recognized, as expressed by ROBERTS and STRUCKMEYER (1938), that the flowering state is a direct result of the internal condition of the plant, rather than a condition brought about by any particular external factor. However, of the external factors which ordinarily influence plants growing under natural conditions, photoperiod and temperature are undoubtedly of primary importance. THOMPSON (1940), in reviewing the work on relation of temperature to vegetative and reproductive development in plants, reports that the evidence shows the prevailing temperature may be a determining factor in photoperiodic response. The present concepts of the mechanisms of photoperiodism have been summarized by MURNEEK (1948), who states that the photoperiodic response is received through the leaves and transmitted to the meristem, and that light, in regard to both duration and intensity, is the activating agent. Various hypotheses to account for the differences in plant reaction to photoperiod have been advanced by CHOLODNY (1939), LANG and MELCHERS (1941), HAMNER (1942, 1944) and BORTHWICK, PARKER and HENDRICKS (1948), but so far there has been no conclusive evidence to warrant the acceptance of any particular proposal.

It has long been recognized that plant varieties or strains within a single species may differ to a considerable degree in their individual time of blooming.

¹ Presented as part of a doctoral thesis to the Faculty of the Graduate School of HARVARD UNIVERSITY in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

However, with the discovery that photoperiod could exert a pronounced influence on time of floral initiation, it soon became evident that varieties of sensitive species differed genetically in their response to photoperiod. GARNER and ALLARD (1930) and BORTHWICK and PARKER (1939) in soybeans, OWEN, CARSNER and STOUT (1940) in sugar beets, OLMSTEAD (1944) in side-oats grama and QUINBY and KAPER (1947) in sorghum have all reported a diversity in photoperiodic response, which was due to genetic variation among those strains within the species studied. Inheritance studies involving photoperiodic response, however, have been relatively few in number. GOODWIN (1944) obtained results from a study of the F_1 and F_2 generations involving three strains of the short-day species, *Solidago sempervirens* L., which indicated that the minimal number of gene pairs determining photoperiodic response approximated the haploid chromosome number ($n=9$). QUINBY and KAPER (1945) reported that three genes exist in the milo variety of grain sorghum which are influenced by photoperiod, and that they are capable of producing four maturity phenotypes under natural day-length conditions. LANG (1948) studied the inheritance of photoperiodic response in *Nicotiana tabacum* L. hybrids, and found that a single gene pair conditions the difference between Maryland-Mammoth, a short-day type, and Java, a day neutral form. However, the rather extreme range encountered in the day-neutral segregates of the F_2 population indicates that modifier genes also influence time of blooming in this group; or perhaps other factors in addition to photoperiod are operative.

It has been known for many years that teosinte is a member of the short-day group of plants, and previous studies have been conducted on the inheritance of this character in maize-teosinte hybrids. COLLINS and KEMPTON (1920) reported that no simple type of inheritance for days to anthesis was indicated by their data obtained from the study of a maize-teosinte F_2 hybrid population. LANGHAM (1940) studied the inheritance of photoperiodic response in crosses of Durango teosinte \times maize, and interpreted the data as indicating a single gene was responsible for the short-day response, and that maize was dominant to teosinte for this character. MANGELSDORF and REEVES (1939) found no linkage of days to anthesis with marker genes on chromosomes 2, 4, 6 and 9 in a study of several backcross progenies of (Florida teosinte \times maize) \times maize. In a study of weak versus strong response to length of day in Nobogame teosinte \times maize and Durango teosinte \times maize F_2 hybrid populations, MANGELSDORF (1947) reported that in neither population was there an approach to a simple Mendelian ratio.

DESCRIPTION OF PRESENT STUDY

Previous investigations have definitely shown that teosinte varieties differ to a considerable degree in their response to photoperiod. Consequently, in order to determine the response of several varieties, as well as to obtain a rather adequate sample of the species, varieties from six different sources were used in this experiment. These varieties, with the exception of El Valle, have been designated by the name of the town near or in which they were collected.

As may be determined from the map shown in figure 1, giving places of origin of the different teosinte varieties, these varieties represent collections from a range of latitudes.

Three of the varieties are from Nobogame, Durango and Chalco respectively in Mexico, and three are of Guatemalan origin. One of the latter is from a collection obtained near San Antonio Huixta, another from a collection made near Jutiapa, and the third is of indefinite origin but resembles very much the commercial type used in the southern United States which is known as the



FIGURE 1.—Map of the southern United States, Mexico and Guatemala, showing original place of collection for each of the teosinte varieties used in the present study. The location of College Station, Texas, where the maize-teosinte hybrids were grown, is also given.

Florida variety. As this latter type, which has been designated as El Valle, is apparently similar to Florida teosinte in all respects, its place of origin has been shown as southern Guatemala, in accord with the conclusion by LONGLEY (1937) as to the source of the Florida variety.

In order to minimize the degree of variability within each of the teosinte varieties, strains with some degree of inbreeding were used whenever possible. S_1 strains of Nobogame, Durango and Jutiapa and an S_2 strain of Huixta were used in all crosses involving these teosintes. An individual open-pollinated plant served as a source of seed of the Chalco variety; the only seed available of the El Valle variety was that from an open-pollinated source.

Since the type of maize used also affects the appearance of the hybrids, a common multiple tester stock was used for making all crosses with the exception of those involving Jutiapa teosinte. The multiple tester was quite uniform as a result of inbreeding, and was homozygous for marker genes on nine of the ten chromosomes. The marker genes were bm_2 , lg_1 , a_1 , su_1 , Y , gl_1 , j_1 , wx and

g_1 . In addition, the marker gene *P* was introduced from the maize parent in some of the crosses. All of the teosinte varieties carried contrasted alleles of these genes.

A typical plant of the multiple tester maize parent is shown in figure 2. A plant of El Valle teosinte shown in figure 3 gives some idea of the difference in appearance of the two species under Texas conditions. The other Guatemalan teosintes resembled El Valle to a marked degree in plant growth, but the Mexican teosintes were considerably less vigorous and possessed fewer tillers. The F_1 hybrid of El Valle teosinte \times maize is shown in figure 4. In the hybrids, also, as in the varieties, the Guatemalan teosintes were considerably more vigorous and produced a greater number of tillers than the Mexican varieties.

The study of all parental strains and hybrid populations was conducted at College Station, Texas (see figure 1) during the spring and summer of 1948, where the day length during the growing season approaches a maximum of approximately 14 hours. The seeds of each progeny were planted individually in 5-cm high paper cups in the greenhouse on April 17 to 19, and seedlings were transplanted to the field ten days later. Weather conditions in general were favorable from the time of planting until the latter part of July, although from the last week in July until mid-September the growth of all plants was definitely retarded by the hot, dry weather.

In addition to the parental progenies and F_1 hybrids, both F_2 populations and populations involving backcrosses to each parent were included in the experiment. An attempt was made to provide 400 plants in each F_2 population, 200 plants in each backcross, 15 of each of the teosinte parents and F_1 's and 60 of the maize parent. Although seed shortages of certain crosses and unfavorable weather conditions after planting reduced the final number of plants used for study, approximately the desired number was available in most populations. The actual number of individuals in each population is given in table 1. In this table, as in all later tables, the variety of teosinte is used to designate the indicated generation of a cross involving that particular teosinte and maize.

Plants of all populations were examined continually during the period of pollen shedding, and the date of anthesis for each plant recorded. In actual practice it was frequently necessary to estimate the actual date of anthesis for

TABLE 1
Number of individuals in each population.

POPULATION	NOBOGAME	DURANGO	CHALCO	EL VALLE	HUIXTA	JUTIAPA
Teosinte parent	8	8	10	14	13	10
Teosinte-maize F_1	14	14	—	14	11	15
Maize parent	54	54	54	54	54	54
$F_1 \times$ teosinte	179	188	197	148	76	114
$F_1 \times$ maize	195	188	194	145	196	171
Teosinte-maize F_2	372	377	354	384	381	221



FIGURE 2.—Plant of the multiple tester maize parent.



FIGURE 3.—Plant of El Valle teosinte.



FIGURE 4.—Plant of the F_1 hybrid El Valle teosinte \times maize.

plants blooming during the latter half of the summer. During this period, because of insufficient moisture and extremely hot weather, the anthers did not usually dehisce, and in many instances the tassels were formed but failed to emerge fully. There were some plants, particularly in the F_2 and teosinte backcross populations involving Huixta teosinte, that lived until September 1 or later and finally died without forming tassels. Their dates of anthesis were recorded as the time at which they died. While this procedure introduced some error, it seemed to be the best method to follow in the recording of the data. All plants so classified were of a very late group (135 days or more) for their population, so it is not felt that they were seriously misclassified.

Some difficulty was encountered in determining the exact date of anthesis for the teosinte parents, as all tended to flower during the latter part of the season when growing conditions were poor. Several plants of both the Nobogame and El Valle parents actually shed pollen, so the dates recorded for these varieties are accurate for the conditions encountered in 1948. Of the Jutiapa and Durango parental plants only two of each variety formed tassels, but as the duration of growth for several other plants indicated a similar period to flowering the estimates for those varieties should be relatively accurate. No plants of the Chalco and Huixta teosintes formed visible tassels, so their estimated dates of anthesis are based on the length of life of the latest plants of each variety. It is felt that the adverse growing conditions during the latter part of the season lengthened the time to flowering for late plants of all populations as well as the parental teosintes, and that under more favorable conditions the extremes in lateness would not have been quite so great.

In addition to the information obtained on date of anthesis for plants in all populations, data were also collected on number of tillers. Most teosinte varieties, and particularly those of Guatemalan origin, are characterized by a large number of tillers. On the other hand, most maize varieties tiller very little, and the strain used in this study exhibited no tendency whatsoever for tillering.

SEGREGATION OF MARKER GENES

Numerous studies have been conducted using marker genes in maize-teosinte crosses, and in most instances a normal segregation has occurred. However, KEMPTON (1924) in studying a hybrid of maize and Florida teosinte recovered only 12 percent of the *br* plants in the F_2 generation instead of the expected 25 percent. MANGELSDORF and REEVES (1939) reported a marked deficiency of plants segregating for the *su*₁ and *Tu* genes on chromosome 4, in a backcross population of (Florida teosinte \times maize) \times maize.

Segregation of marker genes in the backcrosses to maize and the F_2 populations which occurred in the present experiment are shown in tables 2-6. Chi-square values were calculated for goodness of fit to a 1:1 and 3:1 ratio for the backcross and F_2 progenies respectively, and P values for all genes are included in the tables. Although most of the genes behaved in a normal fashion, there were a few notable exceptions. The most striking deviation was found in the sugary segregates of the El Valle backcross and F_2 progenies. Of the seed on the backcross ears only 13.4 percent were sugary, while on the F_2 ears

TABLE 2

Segregation of marker genes in Nobogame teosinte-maize populations.

CHROMOSOME	GENE	F ₁ ×MAIZE			F ₂		
		TEOS. GENE	MAIZE GENE	P VALUE	TEOS. GENE	MAIZE GENE	P VALUE
1	<i>Bm</i> ₂	87	108	.15	272	100	.40
1	<i>P</i>	—	—	—	29	45	< .01
2	<i>Lg</i> ₁	107	88	.25	283	89	> .50
3	<i>A</i> ₁	85	110	.10	232	140	< .01
4	<i>Su</i> ₁	149	180	.10	738	185	< .01
6	<i>Y</i>	152	177	.15	200	723	.02
7	<i>Gl</i> ₁	89	106	.20	273	99	.25
8	<i>J</i> ₁	100	95	> .50	319	53	< .01
9	<i>Wx</i>	165	164	> .50	683	240	.50
10	<i>G</i> ₁	89	106	.20	288	84	.20

8.0 percent were sugary. These results agree with those of previous investigators in demonstrating a deficiency of fourth chromosome maize genes in hybrids with Florida teosinte, a fact which gives additional support to the assumption that the El Valle and Florida varieties are quite similar. Although the cause of this deficiency cannot be determined from this experiment, it seems reasonable to conclude that it is related to the sterility which is found in the F₁ hybrids. BEADLE (1932), MANGELSDORF and REEVES (1939) and O'MARA (1942) have all reported pollen sterility in hybrids of Florida teosinte and maize. The exact mechanism causing this sterility is unknown, although it seems rather certain, according to the results of previous experiments by ROGERS (unpublished), that some factor on chromosome 4 is primarily responsible for this sterility which occurs in hybrids of the southern Guatemalan teosintes with maize.

TABLE 3

Segregation of marker genes in Durango teosinte-maize populations.

CHROMOSOME	GENE	F ₁ ×MAIZE			F ₂		
		TEOS. GENE	MAIZE GENE	P VALUE	TEOS. GENE	MAIZE GENE	P VALUE
1	<i>Bm</i> ₂	101	87	.30	277	100	.50
1	<i>P</i>	29	63	< .01	46	112	.25
2	<i>Lg</i> ₁	103	85	.20	270	107	.10
3	<i>A</i> ₁	96	92	> .50	255	122	< .01
4	<i>Su</i> ₁	148	132	.30	642	179	.04
6	<i>Y</i>	152	128	.15	226	595	.10
7	<i>Gl</i> ₁	117	71	< .01	340	37	< .01
8	<i>J</i> ₁	104	84	.15	275	102	.30
9	<i>Wx</i>	133	147	.40	622	199	> .50
10	<i>G</i> ₁	116	72	< .01	284	93	> .50

TABLE 4

Segregation of marker genes in Chalco teosinte-maize populations.

CHROMOSOME	GENE	F ₁ ×MAIZE			F ₂		
		TEOS. GENE	MAIZE GENE	P VALUE	TEOS. GENE	MAIZE GENE	P VALUE
1	<i>Bm₂</i>	86	108	.10	258	96	.35
1	<i>P</i>	39	68	< .01	54	100	< .01
2	<i>Lg₁</i>	92	102	.50	272	82	.40
3	<i>A₁</i>	111	83	.05	243	111	< .01
4	<i>Su₁</i>	174	136	.04	725	168	< .01
6	<i>Y</i>	115	123	> .50	246	647	.10
7	<i>Gl₁</i>	111	83	.05	274	80	.30
8	<i>J₁</i>	114	80	.02	267	84	> .50
9	<i>W_x</i>	157	153	> .50	674	219	> .50
10	<i>G₁</i>	107	87	.15	282	72	.05

There is a marked deficiency of glossy segregates in those populations involving Durango teosinte. In the maize backcross 37.8 percent glossy plants were recovered, while only 9.8 percent were obtained in the F₂ population. A similar deficiency of glossy plants occurred in the Huixta teosinte-maize F₂ population, as only 14.2 percent were obtained. However, in the (Huixta teosinte×maize)×maize population this gene pair segregated in a normal 1:1 ratio. In previous studies of Durango teosinte-maize hybrids involving marker genes on chromosome 7 no deficiencies of the maize genes have been reported in the segregating populations. This deficiency of chromosome 7 maize genes found in the populations studied in this experiment, therefore, is not typical of all maize-teosinte hybrids, and does not always occur even in crosses of maize with the same variety of teosinte.

TABLE 5

Segregation of marker genes in El Valle teosinte-maize populations.

CHROMOSOME	GENE	F ₁ ×MAIZE			F ₂		
		TEOS. GENE	MAIZE GENE	P VALUE	TEOS. GENE	MAIZE GENE	P VALUE
1	<i>Bm₂</i>	74	71	> .50	277	107	.20
2	<i>Lg₁</i>	64	81	.15	286	98	> .50
3	<i>A₁</i>	91	54	< .01	289	95	> .50
4	<i>Su₁</i>	194	30	< .01	460	40	< .01
6	<i>Y</i>	75	149	< .01*	139	361	.15
7	<i>Gl₁</i>	76	69	> .50	278	106	.25
8	<i>J₁</i>	96	49	< .01	306	78	.04
9	<i>W_x</i>	128	96	.04	360	140	.10
10	<i>G₁</i>	82	63	.20	308	76	.02

* Not segregating in 1:1 ratio.

An excess of the double recessive segregates of the a_1 gene on the third chromosome occurred in several progenies. In all F_2 populations, with the exception of the El Valle teosinte-maize hybrid, significant departures from a 3:1 ratio were obtained. The same tendency for an excess of a_1a_1 plants occurred in the backcross populations of Nobogame and Huixta, although there was no such indication in the Durango or Chalco backcrosses. The remaining significant deviations are in all likelihood of a random nature, or have been caused through difficulties in classification. In particular, seeds homozygous for su_1 or y were extremely difficult to classify in the F_2 progenies. The deficiencies of j_1j_1 plants found in several populations were in all probability brought about

TABLE 6
Segregation of marker genes in Huixta teosinte-maize populations.

CHROMOSOME	GENE	$F_1 \times \text{MAIZE}$			F_2		
		TEOS. GENE	MAIZE GENE	P VALUE	TEOS. GENE	MAIZE GENE	P VALUE
1	Bm_2	82	114	.02	290	91	> .50
1	P	—	—	—	42	113	.50
2	Lg_1	87	109	.10	278	103	.35
3	A_1	81	115	.02	261	120	< .01
4	Su_1	123	134	.50	679	185	.02
6	Y	107	150	< .01	257	607	< .01
7	G_1	95	101	> .50	327	54	< .01
8	J_1	93	103	> .50	316	65	< .01
9	Wx	120	137	.30	661	203	.40
10	G_1	116	80	.01	110	28	.20

through a failure to identify this character in every instance. As plants homozygous for g_1 are usually weak, the deficiencies of this character probably resulted from a loss of such plants at germination or in the early seedling stage.

RESPONSE TO PHOTOPERIODISM

Previous investigations have shown that all teosinte varieties are sensitive to photoperiod, although there is considerable variation among the different varieties in the strength of their response. The results of EMERSON (1924), LANGHAM (1940) and O'MARA (1942) show that the Mexican teosintes will bloom much earlier than the Guatemalan teosintes, when both are subjected to a 10-hour photoperiod. North American maize is rather insensitive to photoperiod, although EMERSON (1924) and LANGHAM (1940) found that late types of maize from the more southern latitudes respond to photoperiod. BRUNSON (cf. LANGHAM 1940) has also reported a late-flowering type of maize, *cz*, which has an indefinite vegetative growth under field conditions, but can be brought into flowering under short-day conditions. The maize stock used in this experiment is adapted to the northern United States, and represents an early type which is insensitive to photoperiod.

The mean number of days to anthesis of each population is shown in table 7, and a measure of variation for each population is given as the standard error of the mean. The maize parent bloomed in approximately 58 days, while even the earliest teosinte variety required more than 100 days. The Mexican teosintes as a group flowered much earlier than the Guatemalan teosintes. There is an increase in mean number of days to anthesis as the percentage of teosinte germplasm increases within any group of progenies involving a particular teosinte.

The F_1 hybrids of the Mexican teosintes bloomed at approximately the same time as the maize parent, indicating that maize is almost completely

TABLE 7
Mean number of days to anthesis of each population.

POPULATION	NOBOGAME	DURANGO	CHALCO	EL VALLE	HUIXTA	JUTIAPA
Maize parent	58.2±0.40	58.2±0.40	58.2±0.40	58.2±0.40	58.2±0.40	58.2±0.40
F_1 ×maize	57.0±0.32	58.2±0.41	61.5±0.45	71.6±1.06	67.6±0.50	66.6±0.75
Teosinte-maize F_1	60.9±1.10	64.9±0.72	—	102.0±3.29	106.2±5.25	126.7±2.84
Teosinte-maize F_2	65.4±0.46	70.9±0.52	74.7±0.59	112.5±1.51	131.2±1.49	115.5±2.08
F_1 ×teosinte	74.7±1.00	87.0±1.07	94.4±0.70	172.9±0.96	178.3±1.04	175.7±1.23
Teosinte parent	110.4	137.5	146.0*	199.6	207.0*	206.2

* Actual date of blooming estimated.

dominant to these teosintes in photoperiodic response. Although no seed of the Chalco teosinte-maize F_1 was available to permit inclusion of this hybrid in the experiment, previous observations indicate that the Chalco teosinte-maize hybrid blooms at approximately the same time as the Durango teosinte-maize hybrid. The Guatemalan teosinte-maize F_1 hybrids flowered somewhat later than the maize parent. Apparently maize is incompletely dominant to this group of teosintes, since the mean number of days to anthesis of each of these F_1 hybrids approached the maize parent more closely than it did the teosinte parent. The rather wide range of blooming dates of these F_1 plants suggests that they are quite easily affected by environmental conditions. The mean blooming date of each of the (teosinte×maize)×maize populations approached the mean blooming date of the maize parent. The F_2 hybrids on the average bloomed slightly later than the F_1 hybrids, with the exception of the Jutiapa teosinte-maize cross. The (teosinte×maize)×teosinte progenies involving the Mexican teosintes were somewhat intermediate between the F_1 and the teosinte parent, but the Guatemalan teosinte backcrosses rather closely approached the teosinte parent.

The length of the photoperiod at College Station during that part of the year in which the populations were grown is given in figure 5. The hours of sunshine possible are shown for number of days from planting, as well as for time of year, so that the length of the photoperiod at which plants of any population flowered may be readily determined. The frequency distributions for number of days to anthesis of each population are shown in figures 6–11. The plants have been grouped by 5-day intervals rather than by daily inter-

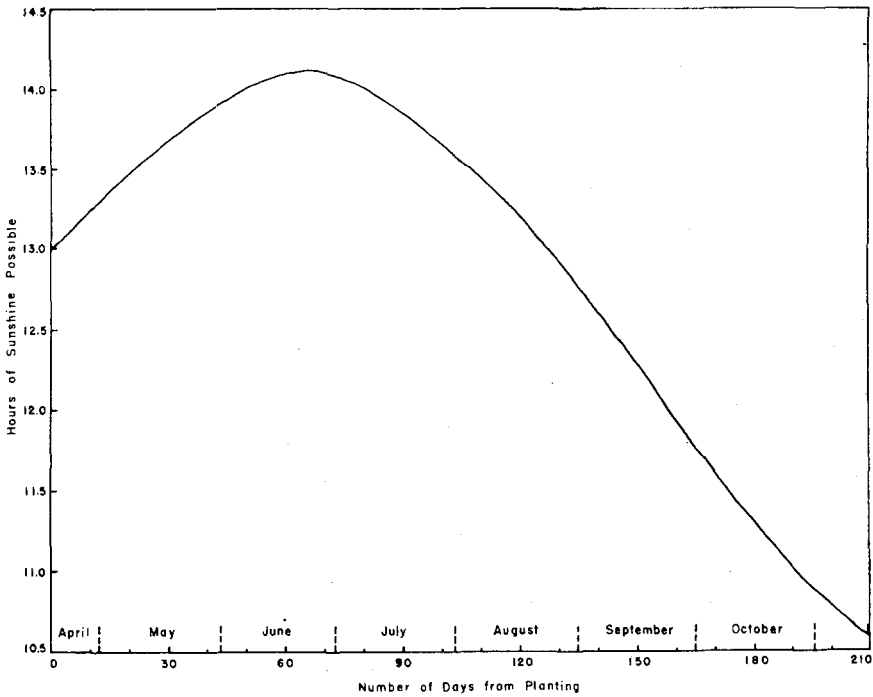


FIGURE 5.—The number of hours between sunrise and sunset during the growing season of the maize-teosinte hybrids at College Station, Texas.

vals in plotting their blooming dates. This grouping, however, has had no effect on the general appearance of the curves beyond smoothing out some of the irregularities.

These data show that the behavior of corresponding populations of each of the Mexican teosintes was quite similar. Likewise, the populations involving the Guatemalan teosintes, although differing from those of the Mexican teosintes, were quite alike in their behavior. Obviously the Mexican teosintes represent slight variations of a certain type of photoperiodic response, and the Guatemalan teosintes represent a group with a considerably stronger response.

The populations derived from Nobogame teosinte definitely show the weakest response to short day of any of the populations studied. The maize backcross progeny bloomed on the average slightly earlier than the maize parent, and both populations have a very pronounced mode at the same interval of 55–59 days. The F_2 mode is only slightly later than that of the maize backcross, occurring at the next interval of 60–64 days. Even the (teosinte \times maize) \times teosinte progeny exhibits a very weak response to length of day, most of the plants falling within the same range as those of the F_2 population. Apparently the day length of 13–14 hours, which prevailed during the growing season, is only slightly above the critical photoperiod for this particular variety of teosinte.

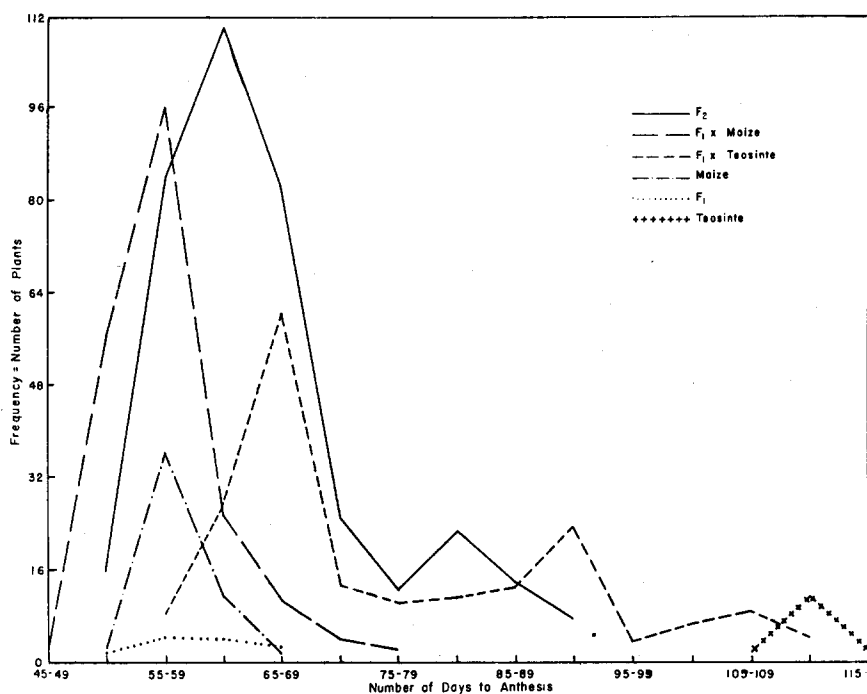


FIGURE 6.—Frequency distribution for number of days to anthesis in maize and all populations involving Nobogame teosinte.

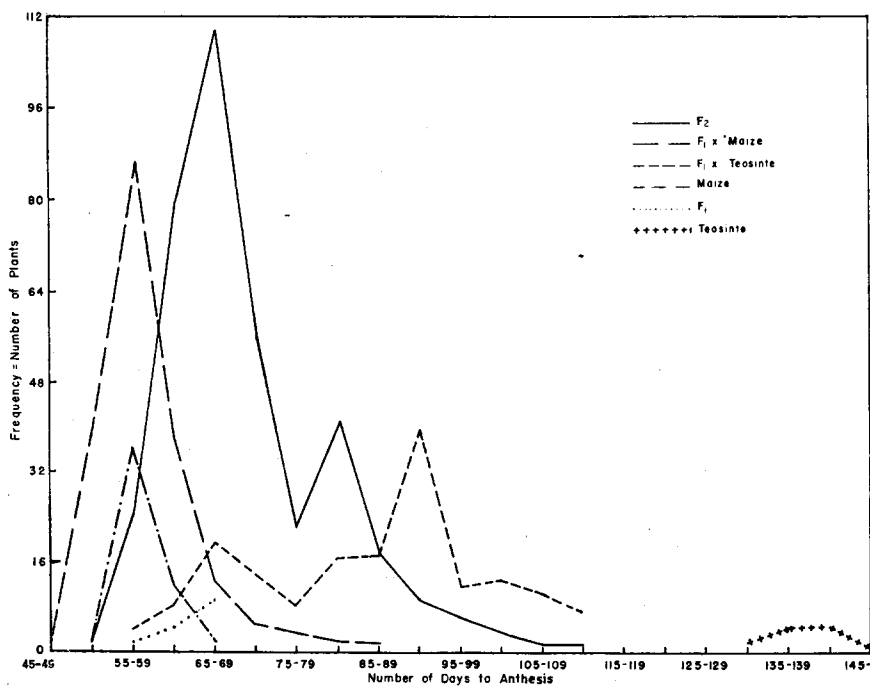


FIGURE 7.—Frequency distribution for number of days to anthesis in maize and all populations involving Durango teosinte.

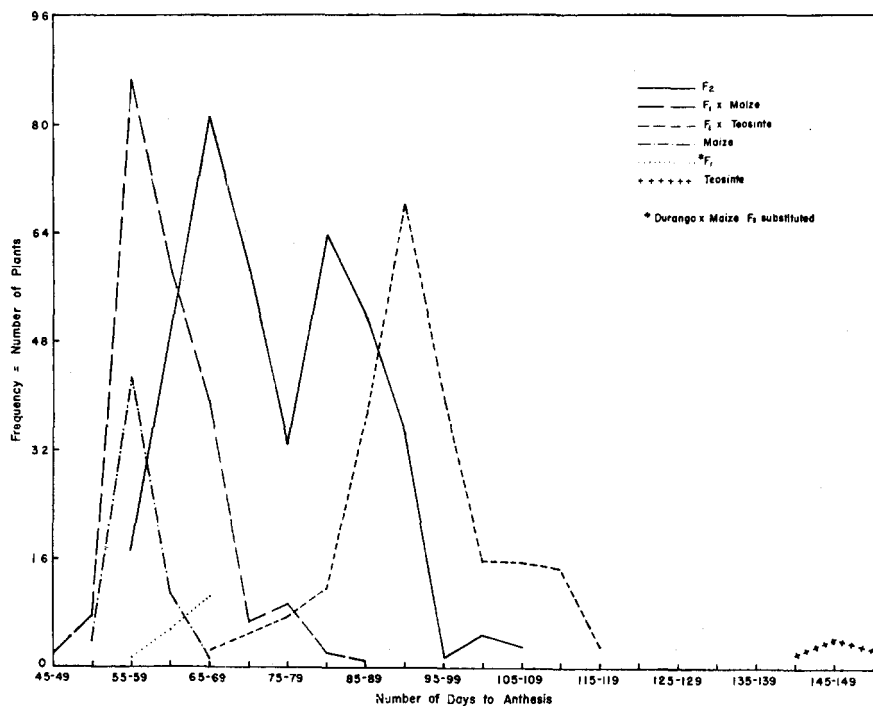


FIGURE 8.—Frequency distribution for number of days to anthesis in maize and all populations involving Chalco teosinte.

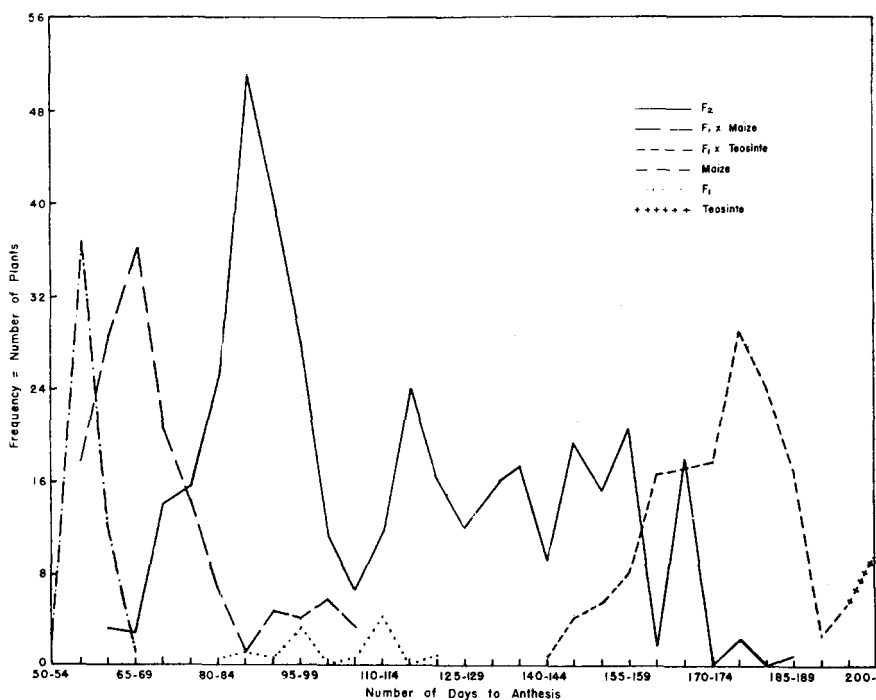


FIGURE 9.—Frequency distribution for number of days to anthesis in maize and all populations involving El Valle teosinte.

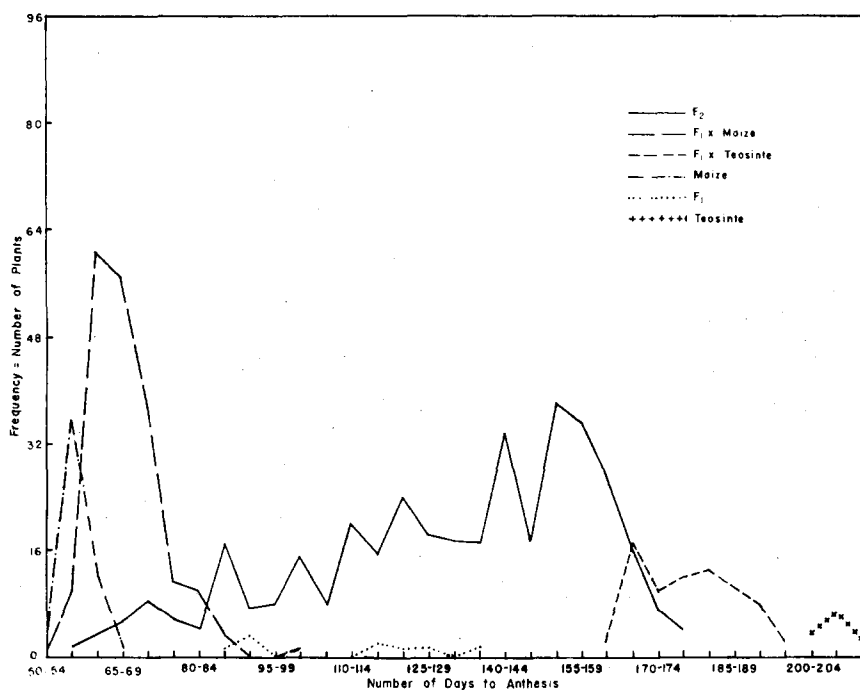


FIGURE 10.—Frequency distribution for number of days to anthesis in maize and all populations involving Huixta teosinte.

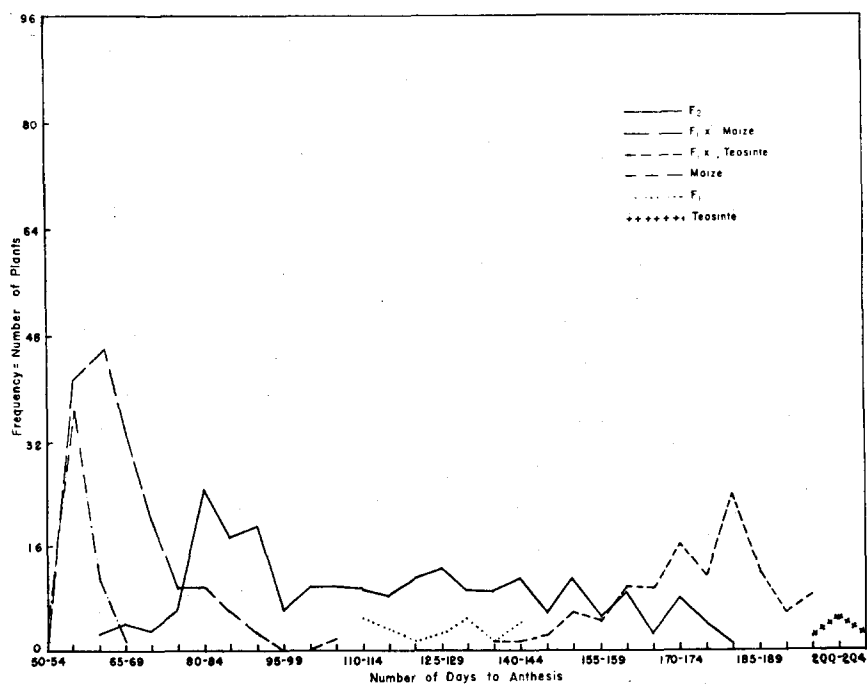


FIGURE 11.—Frequency distribution for number of days to anthesis in maize and all populations involving Jutiapa teosinte.

The Durango and Chalco hybrid populations responded in much the same manner under the conditions of this experiment. The maize backcross of each variety exhibits little variation, and the mode for each population occurs at 55–59 days. The F_2 hybrids of the two varieties also have the same mode of 65–69 days. However, the Chalco F_2 population is noticeably more variable and contains a higher proportion of late plants than the Durango F_2 population. The (teosinte \times maize) \times teosinte populations for both strains are somewhat intermediate between the F_1 and each parent. The Chalco population in particular has a definite mode approximately midway between the F_1 and Chalco teosinte. Although both the Durango and Chalco progenies approach the F_1 to a greater extent than they do the teosinte parent, this is probably caused to a large degree by the extreme growing conditions to which the teosinte parents were subjected.

The data clearly show that there is a definite sequence among the Mexican teosintes in the strength of their response to length of day. Nobogame shows the weakest response of the three teosintes, Chalco the strongest, and Durango is intermediate between the two. Segregation in all populations definitely shows, that for the photoperiod under which the experiment was conducted, the weak response to photoperiod of the maize parent is completely dominant, or almost so, to the strong response of the Mexican teosintes. There is, however, no evidence of simple Mendelian inheritance for this character in any population involving the Mexican teosintes.

The reaction of the Guatemalan teosintes in all progenies indicates that they possess a comparable genetic complex for photoperiodic response. Like the Mexican teosintes they exhibit a slightly variable response within this common behavior pattern, although the exact sequence among these varieties is not so clear. Considering all segregating populations, however, there seems little doubt but that the Huixta variety shows the strongest response of the Guatemalan teosintes.

The maize backcross progenies of all of these varieties strongly approach the maize parent, although a few plants overlap the range of the F_1 progenies. This distribution indicates dominance of the maize parent, although not of the almost complete type found in the Mexican teosinte crosses. The segregation in all of the Guatemalan teosinte-maize F_2 hybrids is quite pronounced, an extremely wide range occurring in all progenies. However, in the El Valle and Jutiapa populations the modal blooming date occurs near the blooming period of the maize parent, and in the Huixta progeny the majority of the plants approach the teosinte parent in time of flowering. The behavior of these F_2 populations, under the prevailing photoperiod, indicates that maize is partially dominant to the El Valle and Jutiapa varieties for photoperiodic response, but that the Huixta variety is partially dominant to maize for this character.

The distribution of blooming dates in the teosinte backcrosses is quite consistent for all of the Guatemalan varieties. These progenies show only a moderate degree of segregation, and approach the teosinte parent in each instance. This is a rather interesting occurrence in view of the fact that the maize backcross progenies of these same teosintes approach the maize parent

in time of flowering. These results rather definitely show, that regardless of the parent to which the backcross is made, the resulting progeny will display the flowering habits of the recurrent parent.

A rather striking abnormality noticed in plants of several segregating populations was a type of vegetative tassel. This unusual condition of the tassel was particularly noticeable in the Huixta teosinte-maize F_2 and the backcross of (Chalco teosinte \times maize) \times Chalco teosinte. One of the more pronounced types of vegetative tassel from the Chalco backcross progeny is illustrated in figure 12. As may be seen from the photograph this condition is characterized



FIGURE 12.—Vegetative tassel from the (Chalco teosinte \times maize) \times Chalco teosinte population.

by the development of vegetative rather than floral organs in the spikelet. A condition similar to this has been previously described in both maize and teosinte by REEVES and STANSEL (1940) and in maize by COLLINS (1909).

The occurrence of these vegetative tassels indicates that some plants may actually revert to a vegetative state after a certain degree of floral initiation. It seems reasonable to assume that for these plants the photoperiod was such as to induce originally formation of flowering primordia, but subsequent conditions altered the normal development of the staminate inflorescence to cause it to revert to a vegetative state. Perhaps such plants did not experience the required photoperiod for a sufficient period of time to permit normal development of the floral parts. LOEWING (1939), in discussing the difference in photoperiod required for flowering and fruiting stages, suggests that the

photophase of plant development be divided into 1) an initial flowering phase and 2) a gametogenic phase. If they may be so divided, the behavior of the above mentioned plants may be explained by assuming that they received the correct photoperiod for floral initiation but not for the gametogenic phase.

NUMBER OF TILLERS

A difference in number of tillers is one of the characteristics which, like response to photoperiod, usually distinguishes maize from most varieties of teosinte. Since tillering is associated with photoperiodism in teosinte varieties, and since both are affected by the internal and environmental forces influencing the vegetative and reproductive stages, it seemed desirable to determine whether the same chromosomes are involved in the inheritance of tillering and photoperiodism.

Although there are types of maize which may tiller as profusely, or even more so, than some varieties of teosinte, most of the present-day varieties of field maize commonly grown in the United States evidence little tendency for tillering. A glance at the data in table 8 reveals that the maize stock used in this experiment produces no tillers, and that the teosinte varieties exhibit

TABLE 8
Mean number of tillers of each population.

POPULATION	NOBOGAME	DURANGO	CHALCO	EL VALLE	HUIXTA	JUTIAPA
Mazie parent	0	0	0	0	0	0
F ₁ ×maize	1.89±.08	2.22±.13	0.91±.08	2.41±.16	1.60±.10	2.37±.11
Teosinte-maize F ₁	2.00±.42	2.79±.39	—	4.07±.63	3.82±.40	3.93±.47
Teosinte-maize F ₂	3.29±.10	3.22±.11	1.08±.06	4.08±.13	3.20±.10	5.38±.24
F ₁ ×teosinte	4.51±.13	4.33±.16	1.28±.08	9.71±.41	10.13±.39	8.78±.53
Teosinte parent	5.38±.42	4.88±.48	1.10±.53	14.14±.98	10.92±.89	8.50±1.06

varying degrees of tillering. All of the Guatemalan teosintes show a strong tendency for tillering, while the Durango and Nobogame varieties tiller moderately. The Chalco variety is quite similar to maize in this character, producing on the average slightly more than one tiller per plant. A consistent feature of all progenies involving a particular teosinte is an increase in mean number of tillers with an increase in percentage of teosinte germplasm.

The Nobogame and Durango teosintes behave very much alike in their effect on tiller number in the different hybrids with maize. The mean tiller number of the F₁ and F₂ populations of each variety is approximately intermediate between the two parents, and the mean of each backcross population falls between the mean of the F₁ hybrid and the recurrent parent. However, the means of these segregating populations do indicate some degree of dominance for the tillering habit of the teosinte parent. With the exception of the Nobogame teosinte-maize F₁, the F₁ and F₂ hybrids are closer to the teosinte parent than to the maize parent, and the backcross to teosinte approaches the

teosinte parent much closer than the backcross to maize approaches the maize parent. The degree of tillering in the Chalco hybrids, although much below that of the Nobogame and Durango hybrids, also indicates dominance for the tillering habit of the teosinte parent.

The Guatemalan teosintes show much the same type of behavior they exhibited for photoperiodic response. All varieties react in the same general manner in the different hybrids with maize, and from the behavior of the F_1 and F_2 progenies, the maize parent appears to be partially dominant to the teosinte parent. The mean number of tillers for each of the F_1 and F_2 populations including the Guatemalan teosintes, with the exception of the Jutiapa teosinte-maize F_2 , is closer to the mean of the maize parent than to the mean of the teosinte parent.

The backcrosses to maize involving the Guatemalan varieties are somewhat intermediate between the F_1 and the maize parent, and exhibit a rather limited degree of tillering. The backcrosses to teosinte on the other hand tiller profusely, and approach the teosinte parent very closely in mean number of tillers. Here again, as in the response of these same hybrids to photoperiod, the backcross progeny displays the habit of the recurrent parent. This parallel behavior of the two characters is not surprising, since vegetative growth in plants, and hence production of tillers, is strongly affected by length of the growing period.

LINKAGE RELATIONS OF MARKER GENES WITH PHOTOPERIODIC RESPONSE AND TILLER NUMBER

A study of the linkage relations of marker genes with photoperiodic response and tiller number offers one of the most promising methods of determining the genetic nature of these two quantitative characters. Results of such a study not only give some idea of the number of factors that may be involved in the expression of such characters, but also serve to identify the chromosomes on which genes controlling the characters may occur. Linkage relations between the quantitative characters studied and the marker genes were determined for each maize backcross and F_2 population with the exception of those involving the Jutiapa variety. In testing for linkages between the qualitative marker genes and the quantitative teosinte characters, the group comparison method for classes of different size, as outlined by SNEDECOR (1946), was followed. With the use of this method a comparison was made between those segregates carrying the maize allele and those carrying the teosinte allele. The existence of linkage has been considered as established in those instances where the difference between the means of the two groups (maize allele versus teosinte allele) is significant, and the deviation is in the proper direction to indicate a linkage.

A summary of the linkage relations between photoperiodic response and the marker genes for each population is given in table 9, and the same data for tiller number are included in table 10. These tables contain the linkage

data for both the maize backcross and F_2 populations involving each of the teosinte varieties. Two symbols were used to denote the certainty of the linkages. Obviously more reliance may be placed on those relationships which have proven significant at the .01 level, than on those significant at only the .05 level. Strong deviations suggesting linkage, even though the differences were not quite significant at the .05 level, have likewise been indicated. Any significant deviations not due to linkage have also been included.

TABLE 9

Linkage relations of photoperiodic response with marker genes on nine chromosomes of maize, for each maize backcross and F_2 population involving different varieties of teosinte.

CHROM.	GENE	NOBOGAME		DURANGO		CHALCO		EL VALLE		HUIXTA	
		BC	F_2	BC	F_2	BC	F_2	BC	F_2	BC	F_2
1	Bm_2	—	S	—	—	—	+	—	S	I ^s	—
1	P	—	—	—	—	—	+	—	—	—	—
2	Lg_1	—	—	—	—	—	—	++	—	+	+
3	A_1	S	I ^s	—	—	—	S	—	—	—	—
4	Su_1	S	S	—	—	—	—	—	—	—	—
6	Y	—	—	—	—	+	+	I	+	—	—
7	Gl_1	—	—	—	—	—	—	+	—	—	—
8	J_1	—	—	—	—	+	++	+	++	++	+
9	W_x	I ^s	—	—	—	—	—	—	—	—	—
10	G_1	—	—	—	+	++	++	++	++	I	++

++ = Strong linkage, $P < .01$.

+ = Linkage, $P = .05-.01$.

I = Indication of linkage.

— = Independent inheritance.

S = Strong deviation not due to linkage, $P < .01$.

I^s = Deviation not due to linkage, $P = .05-.01$.

The data conclusively show that genes controlling response to short day are located on chromosome 10 of all teosintes studied with the exception of Nobogame, and on chromosome 8 of all varieties except Nobogame and Durango. Chromosome 6 of Chalco and El Valle also carries genes influencing response to day length. Genes affecting this character definitely occur on chromosome 2 of Huixta, and perhaps on chromosome 2 and 7 of El Valle and chromosome 1 of Chalco. The linkages for all teosintes were usually consistent in both the maize backcross and F_2 progenies, although in some instances a linkage was obtained in only one of the two progenies of a particular variety. The results for short day response obtained in this experiment agree in part with those of MANGELSDORF (1947), who reported that chromosome 10 and perhaps chromosome 8 were involved in response to length of day.

It should also be noted that deviations in the wrong direction for linkage with the strong response for short day occur in several of the populations. This is particularly true in the Nobogame hybrids, where marker genes on chromosomes 3 and 4 show deviations in both the maize backcross and F_2

populations. The deviations for the marker gene on chromosome 4 may be accounted for by the slowness in growth of the su_1 plants, but there may actually be factors for earliness on chromosome 3 of Nobogame which produce what appears to be a reverse linkage. The occurrence of a significant deviation of this same type for the marker gene on chromosome 3 in the maize-Chalco F_2 lends additional support to this assumption that chromosome 3 of some varieties may possess earliness factors. As the other deviations in the wrong

TABLE 10

Linkage relations of tiller number with marker genes on nine chromosomes of maize, for each maize backcross and F_2 population involving different varieties of teosinte.

CHROM.	GENE	NOBOGAME		DURANGO		CHALCO		EL VALLE		HUIXTA	
		BC	F_2	EC	F_2	BC	F_2	BC	F_2	BC	F_2
1	Bm_2	+	+	++	+	+	+	++	++	++	++
1	P		—	—	—	—	—				—
2	Lg_1	+	++	++	++	++	—	++	+	++	++
3	A_1	—	—	—	—	—	+	—	—	—	—
4	Su_1	—	++	—	—	—	I ^s	—	—	++	++
6	Y	—	—	+	+	—	—	—	—	—	—
7	Gh_1	++	++	—	++	++	—	++	—	++	++
8	J_1	—	++	—	I ^s	—	—	—	—	—	—
9	Wx	+	—	—	—	—	—	—	—	—	—
10	G_1	—	++	—	—	—	—	—	—	—	—

++ = Strong linkage, $P < .01$.

+ = Linkage, $P = .05-.01$.

— = Independent inheritance.

I^s = Deviation not due to linkage, $P = .05-.01$.

direction are those for the marker gene on chromosome 1 in the Nobogame F_2 , El Valle F_2 and Huixta backcross, perhaps factors for earliness are also located on chromosome 1 of several teosinte varieties. The fact that these deviations are limited to a few chromosomes affords greater credence to the supposition that earliness factors do exist on chromosomes of the teosinte varieties.

Tiller number shows a linkage with the marker gene on chromosome 1 in all progenies, and a linkage with the marker gene on chromosome 2 in all progenies with the exception of the maize-Chalco F_2 . Genes responsible for tillering are also indicated on chromosome 7 of all varieties, as linkages with the marker gene on this chromosome occur in either one or both of the progenies involving each particular teosinte. The data show that genes affecting tiller number occur on chromosomes 6 of Durango and 4 of Huixta, and possibly on chromosomes 4, 8, 9 and 10 of Nobogame and 2 of Chalco. The different teosintes are unusually consistent in the number of linkages shown by each variety, and also for the particular chromosomes involved in these linkages. These results indicate that each teosinte has approximately the same

number of factors affecting tiller number, with the possible exception of the Nobogame variety for which more are indicated.

Some caution must be exercised before definitely concluding that genes acting on tiller number are located on the chromosomes indicated by the linkage studies. Some of these apparent linkages may be the result of the direct action of the maize gene, as it is known that some recessive genes in maize actually influence the degree of tillering. This may be true in particular for the linkages found on chromosome 2, as it has been previously observed that plants with the liguleless character, which served as a marker for this chromosome, produce fewer tillers than normal liguled plants. The genes *bm₂* and *gl₁*, which served as marker genes for chromosomes 1 and 7 respectively, are less likely to exert a direct effect on the tillering habit, and the significant relationships of these genes with tiller number probably represent actual linkages.

These data clearly show that genes governing each of the particular quantitative characters studied tend to be located on the same chromosomes in each of the varieties. Genes controlling photoperiodic response occur most frequently on chromosomes 8 and 10, and genes for tillering commonly occur on chromosomes 1, 2 and 7.

The average days to anthesis for each class with a different number of tillers were computed for each population, in order to determine whether any relationship existed between the two characters. No correlation was indicated from these calculations, however, as there was no consistent increase in days to anthesis with an increase in number of tillers.

DISCUSSION

Previous investigations on the physiological processes responsible for floral initiation in plants have shown that photoperiod and temperature are the primary factors which influence time of flowering. Individual varieties within a particular species (or closely related species) may differ primarily in their time of floral initiation, therefore, because of their response to either photoperiod or temperature. Differences due to photoperiodic response alone may be obscured by growing all varieties under a day length which is no longer a limiting factor in determining the time at which they flower. If length of photoperiod is thus removed as a limiting factor, and the differences still remain in time of flowering, it seems reasonable to conclude that these residual differences represent variation among varieties in thermal requirements. In other words, even under an inductive photoperiod some varieties take a longer period of time than others to attain the condition essential to floral initiation, and from a genetic standpoint might be regarded as carrying factors for lateness in addition to those affecting response to photoperiod. Previous studies in both maize and teosinte show that differences in time of flowering may still exist among varieties of each species when length of photoperiod is no longer a limiting factor.

Although no extensive experiments have been conducted on photoperiodic

response in maize varieties, the results available indicate that varieties of Central and South America are sensitive to photoperiod. MANGELSDORF (unpublished) has found that varieties from Guatemala, Costa Rica, Colombia and other Central and South American countries, which ordinarily do not flower until October when grown in the vicinity of Boston, are readily forced into flower with short-day treatment. North American varieties on the other hand are affected not at all, or at least very little, by photoperiod, and have apparently become adapted to a long photoperiod through a process of selection. According to HAMNER (1944), "If a given species contains any strains which are especially sensitive to photoperiod and can be classed without question into either the long-day or short-day group, then all of the other strains of the same species will tend to exhibit responses which would place them in the same class. For example, the varieties or strains of some species may be arranged in a graded series, at one end of which the plants are typical short-day plants and at the other end of which the plants are day-neutral or nearly so." As maize varieties apparently form a graded series such as that described above, it seems reasonable to conclude that maize is essentially a short-day species, although certain strains have been developed through a process of selection which are adapted to relatively long photoperiods.

All known varieties of teosinte behave as short-day plants, although the strength of response varies with the variety. Those varieties from Mexico consistently exhibit a weaker response than the Guatemalan varieties, and will also bloom much earlier even under 10-hour photoperiods. LANGHAM (1940) has shown that an early type of maize, such as the multiple gene tester used in the present study, blooms at approximately the same time as the Mexican teosintes when both are subjected to short-day treatment. Although no studies on short-day treatment were included in the present experiment, the behavior of the maize parent and teosinte varieties under short-day conditions in the greenhouse during the winter was similar to that reported by LANGHAM. The maize parent and Mexican teosintes bloomed at approximately the same time, and much earlier than the Guatemalan teosintes.

The inference from these results is that the difference between the maize parent and the Mexican teosinte varieties in time of flowering under long photoperiods must be due to those genes of the Mexican teosintes influencing response to photoperiod. In contrast, although the maize parent seems to differ from the Guatemalan teosintes primarily in those genes responsible for photoperiodic response, other factors which affect floral initiation under even the most favorable inductive photoperiod may also be involved. LANGHAM'S (1940) data on the short-day treatment of Huixta teosinte at different stages of growth throw some light on the factors which influence flowering in this variety. He found that plants in the seedling stage flowered in 101 days after short-day treatment was begun, while plants about six weeks old flowered after a short-day treatment of only 47 days. Apparently the Guatemalan varieties such as Huixta must attain a certain stage of development before short-day treatment is effective. These results suggest that the Guatemalan teosintes possess genes which prevent floral initiation until the plants attain

a certain stage of development, regardless of the length of photoperiod under which they are grown. Perhaps a thermal requirement must first be met before length of photoperiod becomes a limiting factor, and genes governing photoperiodic response become effective.

This study of the maize-teosinte hybrid populations throws some light on the functioning of the genes affecting response to photoperiod. The behavior of the Mexican teosinte-maize hybrids shows that under natural day length in Texas the maize parent is almost completely dominant to this group of teosintes in photoperiodic response. However, LANGHAM's (1940) results indicate that the length of photoperiod may have an effect on the degree of dominance displayed by the maize parent, as in a study of Durango teosinte-maize hybrids at Ithaca, New York, he found that the F_1 hybrids bloomed somewhat later than the maize parent. This suggests that as the photoperiod increases maize is no longer completely dominant to teosinte, and indicates that the teosinte genes governing response to photoperiod are still active in the hybrid, and merely require a higher photoperiod than they do in teosinte to become effective.

The results obtained with the Mexican teosintes show that a very definite relationship exists between the strength of their response to photoperiod and the latitude at which they originated (see map, fig. 1). Also strength of response to photoperiod among these varieties is not completely correlated with other teosinte-like characteristics of the variety. The Chalco variety, which is definitely more maize-like in morphological characters than the Durango variety, exhibits a noticeably stronger response to photoperiod. As teosinte is constantly hybridizing with maize in Mexico, it appears that the maize with which each of the Mexican teosintes has been contaminated may be the controlling factor in their response. This photoperiodic response of the teosinte varieties is what might be expected if the response is primarily determined by maize varieties with which they hybridize, since MANGELSDORF (unpublished) has found that maize varieties also become more responsive to photoperiod as they approach the equator.

The Guatemalan teosinte-maize hybrids bloom much later on the average than the Mexican teosinte-maize hybrids, and the maize genes are not completely dominant to genes of the Guatemalan varieties in photoperiodic response. The wide distribution of segregates in the F_2 populations must be primarily due to those genes controlling photoperiodic response, since the teosinte parents themselves exhibit such a strong response under this same photoperiod. As previously suggested, however, the maize parent and the Guatemalan teosintes may differ by other factors which influence time of flowering, so there may be some segregation due to these factors. The changing photoperiod during the growing season may also have a pronounced effect on this distribution. A study of Guatemalan teosinte-maize hybrids under short-day conditions should provide additional information on the factors distinguishing this group of teosintes and maize in time of flowering.

In the backcross populations involving the Guatemalan teosintes very few of the segregates approach the F_1 hybrid, and the distribution of the segregates

indicates that the proportion of parental germplasm is the primary factor in determining time of flowering. In other words the maize genes are partially dominant in the backcross to maize, while the teosinte genes are partially dominant in the backcross to teosinte. This behavior illustrates a rather unique type of gene action, and cannot be accounted for by either the incomplete type of dominance frequently reported for quantitative characters, or by the pronounced dominance of one parent. The type of behavior occurring in these backcrosses is perhaps best described by the term "antithetical dominance," which was first suggested by ANDERSON and ERICKSON (1941) to explain those cases where the modifiers tend to favor one parental extreme or the other. In the present study the modifiers carried by the maize chromosomes apparently favor the maize genes which have a weak response to photoperiod, while modifiers carried by the teosinte chromosomes favor the teosinte genes which have a strong response. This behavior represents an actual reversal of dominance similar to that described by HARLAND (1932) for the normal versus crinkled character in *Gossypium*, where normal behaves as a dominant in *Gossypium barbadense* L., but is recessive when transferred to *Gossypium hirsutum* L. In these particular maize-teosinte hybrids the strong response of teosinte behaves as a dominant when teosinte germplasm is preponderant, but is more or less recessive when the genetic complex approaches that of maize. Although photoperiodic response is not actually controlled by a single gene, as is the crinkled character reported by HARLAND, the same general type of behavior apparently takes place for each of these characters in species hybrids.

Since photoperiodic response is a rather complex character, and its genetic nature is not completely understood, it becomes rather difficult to develop any precise explanation of the gene action in the two species for this character. The results obtained in the backcross populations might be considered as supporting the theory of dominance proposed by FISHER (1928, 1931), since it seems certain that dominance of the major genes controlling photoperiodic response is conditioned by modifying factors. However, it is difficult to see how this influence of the modifier complex on the dominance of other genes came about as postulated by FISHER: whereby the heterozygote gradually approached the wild type due to the action of modifying factors. Rather, it seems that there has been a selection of numerous genes, perhaps over a considerable period of time, which influence photoperiodic response under the conditions to which each of the species has been subjected. As this character is undoubtedly influenced by numerous genes in each species, this selection actually amounts to the development of a genetic complex which controls photoperiodic response. Therefore, as the genetic complex approaches that of either parent, the type of photoperiodic response also tends to approach that particular parent. As the multiple tester maize parent and the Guatemalan teosintes represent types which are adapted to extremely different conditions, it seems reasonable to conclude that the modifier genes would be selected in each type which favor blooming under the particular photoperiod of their native habitat.

The strong photoperiodic response exhibited by the Guatemalan varieties,

in contrast to that shown by the Mexican varieties, might well be expected because of the shorter days of their natural habitat. However, the response within the Guatemalan group of varieties does not strictly follow latitude, as the Huixta variety, which has the strongest response, occurs at a slightly higher latitude than the El Valle and Jutiapa varieties.

The linkage studies have shown that at least part of the genes responsible for photoperiodic response are found on the same chromosomes in the different varieties, particularly on chromosomes 8 and 10. As genes on these same chromosomes were found in both Mexican and Guatemalan teosintes, they must be genes which control response to photoperiod. It seems reasonable to conclude that these genes, because of their location on the same chromosomes of the different varieties, have had the same origin. Presumably these are also the genes having a major effect on photoperiodic response, although there are probably numerous genes on other chromosomes which have minor effects or which act as modifiers. Those teosinte varieties which exhibit the weaker responses now have either fewer or less effective genes governing response to photoperiod.

The behavior of the segregating populations indicates that the genetic complex of each variety has a pronounced effect on the action of these genes controlling photoperiodic response. Results obtained by HARLAND (1929, 1932, 1936) in studies of *Gossypium* hybrids tend to support this supposition, since he has proved experimentally that the expression of a particular gene may be affected by the modifier complex. He found that genes which segregated in a simple Mendelian ratio when tested within a species display a blending type of inheritance in species hybrids. In further studies he has shown that genes transferred from one species of *Gossypium* to another will have a quite different expression in the two species. For example, the gene for petal spot in *G. barbadense* L. produces a large spot, while in *G. hirsutum* L. the modifier complex causes the spot to be small. It seems quite probable that genes affecting photoperiodic response in certain of the teosinte varieties have lost a part of their effect through the introgression of maize germplasm which possesses modifiers curtailing their expression.

In summarizing these results, the evolution of photoperiodic response in the various teosintes is apparently influenced not only by the infiltration of maize germplasm, but also by the type of maize germplasm. Natural selection in all likelihood influences the development of a type of photoperiodic response best adapted to the particular habitat of each variety. The strong response to short day is not necessarily correlated with other teosinte-like characteristics of each of the varieties studied. In general, photoperiodic response is correlated with the geographical origin of each variety. This might be expected since a similar relationship exists between maize varieties and geographical origin. As this holds true for all except the Huixta variety, apparently this is the least maize-like of the teosinte varieties so far as photoperiodic response is concerned.

It is possible that response to short day does not represent a truly distinguishing characteristic between maize and teosinte, since there may be maize

varieties which exhibit a response to photoperiod as strong as that of teosinte. Response to photoperiod is certainly found in both species, and a considerable range of variation in this character probably occurs in both maize and teosinte. Further investigations on the nature of the photoperiodic response of maize varieties in Central and South America should provide information for a better comparison between the two species in this character.

The tillering habits of the various teosintes included in this study follow in general the same pattern which these varieties exhibit for photoperiodic response. The Guatemalan teosintes are quite similar in tillering behavior, and all show a much stronger tendency for tillering than the Mexican varieties. Within the group of Mexican varieties, however, Chalco teosinte, which exhibits the strongest response to photoperiod, is more maize-like than either Durango or Nobogame in the production of tillers. Degree of tillering in teosinte varieties, therefore, is not necessarily associated with strength of response to photoperiod.

Tillering habit within each of the teosinte varieties, as shown by the behavior of all segregating populations, exhibits no consistent relationship with photoperiodic response, since there is no correlation indicated between tiller number and days to anthesis in any of the populations. In addition, genes controlling tiller number in teosinte occur most frequently on chromosomes 1, 2 and 7, while genes for photoperiodic response are commonly found on chromosomes 8 and 10. The fact that genes affecting tiller number are usually found on the same chromosomes of the different varieties indicates a similar source of genes for this character. However, as these genes are not as effective in some varieties as in others, apparently their effect has been weakened by the introgression of maize germplasm.

SUMMARY

The inheritance of photoperiodic response and tillering was studied in several segregating populations of maize-teosinte hybrids. A multiple tester stock carrying marker genes on nine of the ten chromosomes served as the common maize parent in these progenies. Teosinte varieties from three sources each in Mexico and Guatemala were used in these hybrids to provide a representative sample of the species.

Each of the teosinte varieties exhibits a definite response to photoperiod, although the Guatemalan teosintes show a much stronger response than the Mexican teosintes. The weak response of the maize parent is almost completely dominant in all crosses with the Mexican teosintes, but the Guatemalan teosinte-maize crosses show an intermediate type of behavior indicating that neither parent is completely dominant. This differential response of the various teosinte varieties is probably due in a large part to the action of modifier genes which each carries. The behavior of the backcross populations involving the Guatemalan teosintes suggests that genes responsible for the time of flowering in each species are strongly favored by modifiers of their own genetic complex.

The distribution of plants in all segregating populations indicates that

several genes are responsible for the photoperiodic response of each of the teosinte varieties. The linkage studies show that at least part of the genes responsible for the photoperiodic response are found on the same chromosomes in the different varieties, particularly on chromosomes 8 and 10. Presumably these genes have had the same origin.

In general, photoperiodic response of the different teosinte varieties shows a definite relationship with the geographical origin of each variety. Since a similar relationship exists between photoperiodic response and geographical origin in maize varieties, it seems likely that the introgression of maize germplasm is an important factor in determining the photoperiodic response of the teosinte varieties.

Number of tillers is largely controlled by genes on the same chromosomes (1, 2, 7) of the different varieties, indicating a similar source of genes for this character. However, these genes are much more effective in the Guatemalan than in the Mexican teosintes, as their effect in the latter group of varieties has apparently been weakened by the introgression of maize germplasm.

Tillering habit and photoperiodic response exhibit no definite relationship in any of the segregating populations, indicating that these two characters are controlled by different genes which are not closely linked.

ACKNOWLEDGMENTS

I am indebted to DR. PAUL C. MANGELSDORF for the many helpful suggestions and criticisms contributed by him during the course of this study. It is indeed a pleasure to acknowledge my sincere appreciation for his guidance and encouragement. I would also like to express my appreciation to DR. R. G. REEVES for his suggestions and criticisms during the preparation of the manuscript.

LITERATURE CITED

- ANDERSON, EDGAR, and R. O. ERICKSON, 1941 Antithetical dominance in North American maize. *Proc. nat. Acad. Sci.* **27**: 436-440.
- BEADLE, G. W., 1932 Studies of *Euchlaena* and its hybrids with *Zea*. I. Chromosome behavior in *Euchlaena mexicana* and its hybrids with *Zea mays*. *Z.I.A.V.* **62**: 291-304.
- BORTHWICK, H. A., and M. W. PARKER, 1939 Photoperiodic responses of several varieties of soybeans. *Bot. Gaz.* **101**: 341-365.
- BORTHWICK, H. A., M. W. PARKER, and S. B. HENDRICKS, 1948 Wave length dependence and the nature of photoperiodism. In *Vernalization and Photoperiodism*, 71-78, Waltham, Mass.: Chronica Botanica.
- CHOLODNY, N. G., 1939 The internal factors of flowering. *Herb. Revs.* **7**: 223-249.
- COLLINS, G. N., 1909 Apogamy in the maize plant. *Misc. Papers, U. S. Nat. Herb.* **12**: 453-455.
- COLLINS, G. N., and J. H. KEMPTON, 1920 A teosinte-maize hybrid. *J. agric. Res.* **19**: 1-37.
- EMERSON, R. A., 1924 Control of flowering in teosinte. *J. Hered.* **15**: 41-53.
- FISHER, R. A., 1928 The possible modification of the wild type of recurrent mutations. *Amer. Nat.* **62**: 115-126.
- 1931 The evolution of dominance. *Biol. Revs.* **6**: 345-368.
- GARNER, W. W., and H. A. ALLARD, 1920 Effect of length of day on plant growth. *J. agric. Res.* **18**: 553-606.
- 1930 Photoperiodic response of soybeans in relation to temperature and other environmental factors. *J. agric. Res.* **41**: 719-735.

- GOODWIN, R. H., 1944 The inheritance of flowering time in a short day species, *Solidago semper-virens* L. Genetics **29**: 503-519.
- HAMNER, K. C., 1942 Hormones and photoperiodism. Symp. on Quant. Biol. Cold Spring Harbor **10**: 49-59.
- 1944 Photoperiodism in plants. Ann. Rev. Biochem. **13**: 575-590.
- HARLAND, S. C., 1929 The genetics of cotton. Part I. The inheritance of petal spot in New World cottons. J. Genetics **20**: 365-385.
- 1932 The genetics of cotton. Part V. Reversal of dominance in the interspecific cross *G. barbadense* L. \times *G. hirsutum* L. and its bearing on Fisher's theory of dominance. J. Genetics **25**: 262-270.
- 1936 The genetical conception of the species. Biol. Rev. **11**: 83-112.
- KEMPTON, J. H., 1924 Inheritance of the crinkly, ramose, and brachytic characters of maize in hybrids with teosinte. J. agric. Res. **27**: 537-596.
- LANG, A., 1948 Beiträge zur Genetik des Photoperiodismus. I. Faktorenanalyse des Kurztag-charakters von *Nicotiana tabacum* "Maryland—Mammut." In Vernalization and Photoperiodism, 175-183. Waltham, Mass.: Chronica Botanica.
- LANG, A., and G. MELCHERS, 1941 Über den hemmenden Einfluss der Blätter in der photoperiodischen Reaktion der Pflanzen. Naturwissenschaften **29**: 82-83.
- LANGHAM, D. G., 1940 The inheritance of intergeneric differences in *Zea-Euchlaena* hybrids. Genetics **25**: 88-108.
- LOEHWING, W. F., 1939 Photoperiodic aspects of phasic development. Science **90**: 552-555.
- LONGLEY, A. E., 1937 Morphological characters of teosinte chromosomes. J. agric. Res. **54**: 835-862.
- MANGELSDORF, P. C., 1947 The origin and evolution of maize. Advances in Genetics **1**: 161-207. New York: Academic Press Inc.
- MANGELSDORF, P. C., and R. G. REEVES, 1939 The origin of Indian corn and its relatives. Texas Agr. Exp. Sta. Bull. **574**: 1-315.
- MURNEEK, A. E., 1948 History of research in photoperiodism. In Vernalization and Photoperiodism, 39-61. Waltham, Mass.: Chronica Botanica.
- OLMSTEAD, C. E., 1944 Growth and development in range grasses. IV. Photoperiodic response in twelve geographic strains of side-oats grama. Bot. Gaz. **106**: 46-74.
- O'MARA, J. G., 1942 A cytogenetic study of *Zea* and *Euchlaena*. Mo. Agri. Exp. Sta. Res. Bull. **341**: 1-16.
- OWEN, F. V., E. CARSNER, and M. STOUT, 1940 Photothermal induction of flowering in sugar beets. J. agric. Res. **61**: 101-124.
- QUINBY, J. R., and R. E. KARPEN, 1945 The inheritance of three genes that influence time of floral initiation and maturity date in milo. J. Amer. Soc. Agron. **37**: 916-936.
- 1947 The effect of short photoperiod on sorghum varieties and first generation hybrids. J. agric. Res. **75**: 295-300.
- REEVES, R. G., and R. H. STANSEL, 1940 Uncontrolled vegetative development in maize and teosinte. Amer. J. Bot. **27**: 27-30.
- ROBERTS, R. H., and B. E. STRUCKMEYER, 1938 The effects of temperature and other environmental factors upon the photoperiodic response of some of the higher plants. J. agric. Res. **56**: 633-678.
- SNEDECOR, G. W., 1946 Statistical Methods. 4th ed. xvi+485 pp. Ames, Iowa: Collegiate Press, Inc.
- THOMPSON, H. C., 1940 Temperature in relation to vegetative and reproductive development in plants. Amer. Soc. Hort. Sci. **37**: 672-679.